

## COMMUNICATION IN ANTS (HYMENOPTERA: FORMICIDAE)

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While watching a colony of ants busily going about their affairs, whether it be in the hot bushveld of the Transvaal or around the kitchen sink of your own home, have you ever wondered how they communicate? In such a large social organisation there must be some method of informing each other when they have found food and where to find it, or warning each other when danger threatens. Do they talk, use sign language, or what? In fact they use smells or odours to communicate. The volatile chemicals produced by ants are known as pheromones. A pheromone can be defined as a substance secreted from a gland and released by an animal for detection and response by others of the same species.

It has been found only in recent years that in the social biology of ants much of their behaviour is released and controlled by pheromones. It is now well known that workers of many species possess trail and alarm pheromones. It has also been established that pheromones are associated with recognition and brood-tending. If foraging ant workers find food that is too large to be carried back to the nest without help, they will first feed, and then immediately return to the nest, depositing a chemical substance along the way on the ground. These chemicals are, appropriately, called trail pheromones.

The glandular origin of ant trail pheromones varies considerably from subfamily to subfamily. In the Formicinae the trail pheromones are produced by the hind gut. Hölldobler and Wilson (1977) found in *Oecophylla longinoda* that odour trails are laid from the rectal gland, a previously unrecognized muscled organ located in the rear of the rectal sac. Trail-laying is achieved by eversion of the rectal gland. In order to lay a trail the ant lowers her abdomen, rotates the terminal segment downward, and extrudes the rectal gland. The gland is then dragged lightly over the substratum, apparently resting on a "sled" composed of two pairs of long bristles that lead back from the upper edge of the acidopore.

Most workers encountering a freshly laid trail respond at once by following it outward from the nest. The workers do not follow a liquid odour trace on the ground. Instead, they move through the vapour created by diffusion of the pheromone into the air. According to Wilson (1971), there is a space, which theoretical calculations show to be semi-ellipsoidal in shape, within which the pheromone is detected by the ants. As recruited workers travel through this "vapour tunnel" they sweep their antennae from side to side, evidently testing the air for odorant molecules. In fact, Wilson

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(1971) points out that they are able not only to detect these molecules in the gaseous state, but also move up gradients of molecular concentration, a process of orientation referred to as osmotropotaxis.

Close observation of ants on a pheromone trail will reveal that certain individuals trail or dab the tips of their abdomens on the substrate, whether it be the ground, a wall or branch of a tree. All the ants can be seen hurrying along the trail, their antennae bent forward, following the pheromone odour; ants that have filled themselves at the food site strengthen the trail when they return to the nest. Provided that there is food in plenty, a large number of workers are recruited to the site and a broad trail is established. However, as the food supply is depleted, fewer ants pass along the trail and, as a result, the odour diminishes and fewer and fewer ants visit the site until eventually the food is finished (Skaife, 1979).

The trail pheromones of the Myrmicinae have different glandular sources. In the genus *Crematogaster* the tarsal glands are the source of the trail substance, while in *Pheidole* and *Solenopsis* it is the Dufour's gland. In the genera *Monomorium*, *Huberia* and *Tetramorium* the glandular source is the poison gland. Wilson (1971) discussed trail-laying in the Fire Ant *Solenopsis saevissima*. He observed that when a worker ant returned to the nest after discovering a food source, it walked at a slower, more deliberate pace with its entire body held closer to the ground. At frequent intervals the sting is extruded, and its tip drawn lightly over the ground surface. As the sting touches the surface, a pheromone flows down from the Dufour's gland and forms the odour trail.

The secretions of the majority of the exocrine glands of ants are associated with defensive or aggressive behaviour. If an ant is attacked or harassed while along a trail, foraging for food, or merely within the confines of the nest, it will release the contents of its glands and any ants in the vicinity detecting the odour will immediately become alarmed. An alarm reaction can take a number of different forms: often a very high concentration of the pheromone makes the ant flee from the source, a lower concentration, however, will attract ants, arousing aggression and attracting assistance.

An alarm pheromone acts as an attractant in its lowest concentration, and the first response shown by other ants is an orientation towards the source. But immediately thereafter they show alarm and typically open their jaws in an aggressive fashion. *Oecophylla* workers raise their abdomens and continue their approach with a somewhat stiff-legged gait, alert and attentive to every movement. *Crematogaster* also raise the abdomen, but behave quite differently: instead of a cautious approach they become frenzied, rushing about in search of the disturbance. *Odontomachus* workers, which hold their jaws wide open when alarmed, readily snap them closed with

an audible click, the force capable of severing the limbs of other insects. A different attitude is adopted by the workers of *Polyrhachis*, which lower the abdomen between the legs. These, and other formicine species, spray mixtures of formic acid and pheromone from the tip of abdomen, and these mixtures have a dual purpose, serving both as defensive substances and as alarm pheromones (Skaife, 1979).

Blum (1974) noted that alarm pheromones possess several functions clearly separate from that of merely causing alarm in workers. The other most important function is that it serves as an attractant. It has been found that high concentrations of the alarm pheromone of the myrmicine *Pogonomyrmex badius* released strong alarm behaviour, whereas low concentrations acted as excellent attractants. It has also been demonstrated that alarm pheromones were utilized by three species of ants as recruitment stimuli when used in conjunction with trail pheromones. For example, workers of the formicine *Camponotus socius* Roger fortify their recruitment trails with an alarm pheromone, formic acid, which is highly effective in attracting excited recruits. Blum (1974) believes that because of their capacity to function as low-level attractants, alarm pheromones have probably been frequently utilized to increase the stimulating efficiency of a recruitment signal.

Another aspect of chemical communication is the manner in which the chemical signals themselves alter in space and time. Bradshaw *et al.* (1979) point out that fundamental to this is the concept of the "active space", as the zone around the point of emission within which the concentration of the chemical stimulus is at or above that required for behavioural response. They point out that in a social context, the relationship between the active spaces of a number of chemical releasers will largely determine the behaviour patterns of responding ants.

Bradshaw *et al.* (1979) found that the mandibular gland secretions of the major workers of the formicine ant *Oecophylla longinoda* released in other major workers a complex pattern of behaviour, including components of alerting, attraction and biting. In a behavioural study they found that all ants within a range of 5-19cm were alerted within 30 seconds of the presentation of the secretion, their rate of locomotion increased, they made short, fast runs with frequent changes of direction, with their mandibles held open and their antennae raised. Within approximately a 5cm range most ants were attracted directly towards the source of the chemicals which were initially repellent at a range of less than 1cm; the ants often circled with mandibles spread and gaster raised from the horizontal. Several ants within 2cm halted, and those near the source of the secretion bit it with their mandibles (Bradshaw *et al.*, 1979). They found that the main constituents of the secretion were hexanal and 1-hexanol, which release alerting and attraction respectively.

Of the thirty or so trace components, they found at least two, 2-butyl-2-octenal and 3-undecanone, act as markers for attack. They point out that the behaviour of ants responding to the mandibular gland secretion in still air can be explained in terms of the behavioural components released by the four principal chemicals. "Hexanal has the most rapidly expanding active space, within which workers are alerted. The active space of 1-hexanol initially expands at about half the rate of the hexanal, and within this the workers are attracted towards the point of deposition of the secretion. The biting markers, 3-undecanone and 2-butyl-2-octenal, are active only in the immediate vicinity of their source" (Bradshaw *et al.*, 1979).

The alarm pheromones of ants have different glandular origins. In species of the subfamilies Formicinae and Myrmicinae it has been established that the mandibular glands in the head and the poison and Dufour's glands in the abdominal tip play an important role in attraction and alarm. Cammaerts-Tricot (1974) found that workers of *Myrmica rubra* deposited an attractive secretion from the Dufour's gland when walking around an ant of another species. If the intruder was not killed, the *M. rubra* worker laid a trail of the poison gland secretion from the intruder to the nest, and then returned to the intruder, laying a trail of the Dufour's gland secretion from the nest. The deposit of Dufour's gland secretion consisted of discrete droplets, applied by intermittent contact of the gaster with the ground, whereas poison gland trails were continuous. The Dufour's gland droplets attracted many fellow workers to the site of the intruder.

Glancey *et al.* (1970) demonstrated in the Fire Ant *Solenopsis invicta* Buren (misidentified as *S. saevissima* (F. Smith) ) that the action of the worker ants in locating, transporting and caring for the brood is induced by a pheromone (or pheromones). They did this by extracting the brood of the ant in cold hexane. The clear extract was then poured over corn cob grits (inert material) which were mixed till the hexane evaporated. The treated and untreated (controls) grits were placed on the foraging platform that served the colony. The ants began immediately to pick up the treated grits and carry them to the nest and, after about an hour, they had removed all the treated grits, but left the untreated. They observed that the ants groomed the treated grits in the nest, rubbed them with their antennae and palpi, and generally appeared to care for them as they did their brood. They also found that the worker ants harvested grits treated with extracts of larvae, but they did not harvest any grits treated with extracts of pupae. Neither the glandular source nor the chemical composition of these pheromones were demonstrated.

Walsh and Tschinkel (1974) demonstrated in *Solenopsis invicta* the presence of a non-volatile brood pheromone that was distributed

evenly over the pre-adult cuticle and whose potency was abruptly reduced with the shedding of the pupal skin at eclosion. They found that the signal was completely lost within 72 hours after death.

The evidence given by Walsh and Tschinkel for the existence of a brood pheromone was the retrieval of skins and larval contents on blotting paper by the worker ants, the persistence of the signal for long periods after death, despite disfigurement of the larval cuticle, and the ability of organic solvents to destroy the signal without visibly altering the cuticle. The reasons given by Walsh and Tschinkel for believing that the brood pheromone is non-volatile and transmits by contact were that the worker ants showed no signs of orientation prior to contacting live brood. Also in an experiment with an olfactometer they obtained only random responses from worker ants, thus demonstrating the pheromone's low volatility. They demonstrated that the cuticle must be contacted to be recognized, by the failure of worker ants to retrieve skins wrapped in extremely thin, porous laboratory tissue.

Brain (1975) conducted a series of experiments on the brood of ants belonging to the genus *Myrmica*. He found the workers were unable to distinguish larvae from pharate pupae, and that both aroused more worker response than either pupae or flaccid or shaved larvae. He found that larval skins elicited a normal response, and by masking portions with varnish showed that the surface signal was widely dispersed. He found that this larval recognition signal was species-specific, at least between *Myrmica rubra* and *M. scabrinodes*. Brian (1975) compared his results on *Myrmica* with those given by Glancey *et al.* (1970) and Walsh and Tschinkel (1974) on *Solenopsis*. He found the points of agreement between *Myrmica* and *Solenopsis* in respect of brood recognition appeared to be: pupae differed from larvae, chemical cues exist, the material is soluble in ether, is widely dispersed over the cuticle, and is of low volatility. The points of disagreement were: the substance is soluble in hexane and methanol in *Solenopsis* but not in *Myrmica*, accessory tactile cues are not important in *Solenopsis*, but are undoubtedly important in *Myrmica*. Also, whereas in *Myrmica* pharate pupae are picked up in preference to pupae, in *Solenopsis* it appeared to be the other way round.

Ants have also developed glands for use in other spheres of communication. They are able to distinguish one another from members of other colonies in that they bear a unique and complex odour; this "colony odour" is thought to be a mixture of chemicals derived from the nest material, objects in the immediate vicinity of the nest, and especially from the food that members of the colony consume. The identity of workers is also maintained by trophallaxis — the exchange of liquids both from mouth and anus by processes of regurgitation and defecation. This lively exchange of food from what has been termed the "social stomach", is encour-

raged by workers, who both beg food and offer theirs to others. However, while in the myrmecioid subfamilies workers frequently engage in the exchange of regurgitated food, in the poneroid subfamilies exchange is either poor or totally absent. It is apparent, therefore, that other mechanisms ensure a uniform odour within a colony, and that these may involve not only odours of the nest and its surroundings, but also the composition of the pheromones in each colony (Skaife, 1979).

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